Morphology, systematics, and distribution of Meoma ventricosa grandis and M. ventricosa ventricosa (Echinodermata: Echinoidea: Brissidae) along Mexican coasts

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Abstract.—Two subspecies of the genus Meoma are known from the coasts of México, Meoma ventricosa grandis and M. ventricosa s.s. These conspicuous spatangoids, easily recognized by their incomplete subanal fasciole, are confined to the tropical region of the American seas and are thus characteristic of this region. The systematics of M. ventricosa grandis and M. ventricosa s.s. are reviewed. A new northern distribution limit is now recognized for M. ventricosa grandis, extending its range to Magdalena Bay, Baja California Sur, México.

Resumen.—En las costas de México, existen dos subespecies del género Meoma: Meoma ventricosa grandis y M. ventricosa ventricosa. Estos conspícuos espatangoides que se reconocen fácilmente por su fasciola subanal incompleta, están confinados a la región tropical de los mares americanos siendo eminentemente característicos de la misma. En este trabajo se revisa la sistemática de las dos subespecies. Por otra parte, se amplia el rango de distribución de Meoma ventricosa grandis hasta Bahía Magdalena, Baja California Sur, México, que es el límite norte de su distribución.

Species of the order Spatangoida live on muddy and sandy bottoms in all oceans, exhibiting wide bathymetric distributions, from the intertidal zone down to 5000 m (Chesher 1970). The family Brissidae Gray, 1855, is represented along the Mexican coasts by 15 species, most of which have wide bathymetric distributions and are abundant in deep waters, they are Brissopsis alta, B. columbaris, B. pacifica, B. atlantica; Plethotaenia spatangoides; Brissus latecarinatus, B. obesus, B. unicolor, B. elongata; Plagiobrissus grandis, P. pacificus; Meoma ventricosa grandis, M. ventricosa ventricosa; Metalia maculosa, M. nobilis and M. pectoralis.

Meoma ventricosa is the most widely dis-

tributed species of brissid in Mexican waters: *M. ventricosa grandis* Gray, 1851 is distributed along the Mexican Pacific coast and *M. ventricosa* s.s. (Lamarck, 1816) in the south east of the Gulf of Mexico and the Caribbean Sea. *M. ventricosa* s.s. is abundant in the Mexican Caribbean Sea, while *M. ventricosa grandis* is scarce within Mexican waters (Caso 1949, 1961, 1983). Their thin test and digging habits make them difficult to collect and preserve with conventional sampling methods.

There are few published works referring to the taxonomy of the genus *Meoma* Gray. Mortensen (1951) mentioned the existence of two recent species of the genus for the American coasts: *Meoma ventricosa* (Lamarck) and *M. grandis* Gray. Chesher (1970) expanded the genus *Meoma* by including a new species. He also considered the previously known recent species as two subspecies of *M. ventricosa: Meoma ventricosa* s.s. and *M. ventricosa grandis.* Although the taxonomic status of these subspecies has been reviewed by Chesher (1970), some aspects of the classification at this level have not yet been completely resolved.

The purpose of this work is to clarify as much as possible the taxonomic status of the subspecies of *Meoma ventricosa* and to document a new distribution range for *M. ventricosa grandis* along the Pacific Coast.

Material and Methods

Measurements of the test of Meoma ventricosa were taken using some of the standard measurements suggested by Chesher (1969, 1970). All measurements were made with vernier calipers to the nearest 0.1 mm. A total of 39 specimens was used in this work and data from 18 specimens were assembled for the statistical analysis (nine of each subspecies). To ameliorate the effects of growth and allometry, specimens of similar sizes of both subspecies were chosen. The range in the test length of M. ventricosa s.s. is from 94.84 to 145.41 mm (\bar{X} 122.06 mm) and M. ventricosa grandis is from 110.25 to 130.81 mm (\bar{X} 119.92 mm). Variations between subspecies were analized by simple and multiple regression analyses. Throughout the study, statistical significance is set at the 95 per cent level using Student's t test values.

A total of 33 measurements was chosen to assess variation in test shape and the characteristics of some important structures. The variables and their abbreviations are defined as follows: test length (TL); test width (TW); test height (H); height of the periproct (AH); width of the periproct (AW); distance from the adoral median section of the subanal fasciole to the periproct (SAFT); width of the base of 5 tubercles for each ambulacra zone (I, II, III, IV, V) located in a perimeter of 20 mm around the apical system (T), and width of the peristome (PW).

Material used in this study is housed in the Laboratorio de Sistemática y Ecología de Equinodermos of the Instituto de Ciencias del Mar y Limnología at the Universidad Nacional Autónoma de México (ICMyL-UNAM).

> Results and Discussion Taxonomy Family Brassidae Gray, 1855 Genus *Meoma* Gray, 1851

Diagnosis.-Large echinoids, with peripetalous fasciole markedly indented between the paired petaloids, forming an acute angle in interambulacra 2 and 3. Test oval, broad, with a moderate frontal depression, high, thick-walled, regularly arched, with highest point almost central. Oral surface flat. Posterior end obliquely directed downwards, truncated. Frontal ambulacrum slightly depressed, with podial pores arranged in 2 regular rows distally. Paired ambulacra sunken, narrow, straight; only the anterior ones are slightly curved backwards at their distal ends. Interporiferous zones narrow, densely covered by small tubercles. Apical system slightly anterior, of the ethmolytic type with 4 genital pores; madreporite prolonged backwards so as to separate the posterior genital and ocular plates. Peristome situated anteriorly, wide, semilunar, slightly sunken. Labrum anteriorly extended, densely covered with tubercles. Large periproct, located at the truncated posterior end of the test and overhung. Sternum short and narrow, densely covered with large tubercles. Long episternum (nearly half the length of sternum). Anal fasciole absent. Subanal fasciole bilobed in Meoma frangibilis and M. cadenati, aborally degenerate in adults of M. ventricosa s.s. and M. ventricosa grandis (only the adoral transverse branch remains differentiated). Five types of pedicellariae: globiferous, tridentate, ophicephalous, triphyllous and rostrate.

Type species:—Meoma grandis = (M. ventricosa grandis Gray, 1851).

In Mexico, this genus is represented by two subspecies: *Meoma ventricosa grandis* (West Coast) and *M. ventricosa ventricosa* (East Coast).

Meoma ventricosa ventricosa (Lamarck, 1816) Figs. 1–3, Table 1

Spatangus ventricosus.—Lamarck 1816: 29; Blainville 1827: 89.

Brissus ventricosus.—Gray 1825: 431.

Meoma ventricosa.—Mortensen 1951: 529; Fontaine 1953: 8; Mayr 1954: 6; Hyman 1955: 548, 556; Madsen 1957: 476; Caso 1961: 309; Kier & Grant 1965: 38; Fischer 1966: U592; Chesher 1969: 72-110.

Meoma ventricosa ventricosa.—Chesher 1970: 737–745; Serafy 1979: 94–98; Pawson 1986: 537; Hendler et al. 1995: 243– 245.

Material examined.-2 specimens, Puer-Morelos, Quintana Roo, México to (20°54'07"N, 86°52'05"W), ICMyL-UNAM 4.95.0; 1 specimen, Puerto Morelos, Quintana Roo, México (20°51'03"N, 86°51'07"W), ICMyL-UNAM 4.95.1; 1 specimen, Puer-Morelos, Quintana Roo, México to (20°50'06"N, 86°52'03"W), ICMyL-UNAM 4.95.2; 3 specimens, north of Cabo Catoche, Ouintana Roo, México (22°32'08"N, 87°06'09"W), ICMyL-UNAM 4.95.3; 3 specimens, north of Cabo Catoche, Quintana Roo, México (22°56'11"N, 87°16'01"W), ICMyL-UNAM 4.95.4; 3 specimens, north of Cabo Catoche, Quintana Roo, México (22°33'01"N, 87°05'9"W), ICMyL-UNAM 4.95.5; 4 specimens, north of Cabo Catoche, Quintana Roo, México (22°32'08"N, 87°06'09"W), ICMyL-UNAM 4.95.6; 1 specimen, northwest of Cabo Catoche, Quintana Roo, México (22°48'06"N, 87°13'07"W), ICMyL-UNAM 4.95.7; 1 specimen, north of Cabo Catoche, Quintana Roo, México (22°56'01"N, 87°16'01"W), ICMyL-UNAM 4.95.8; 4 specimens, northwest of Cabo Catoche, Quintana Roo, México (23°14'09"N, 87°28'02"W), ICMyL-UNAM 4.95.9; 3 specimens, northwest of Cabo Catoche, Quintana Roo, México (23°14'09"N, 87°28'02"W), ICMyL-UNAM 4.95.10; 2 specimens, northwest Isla Contoy, Quintana Roo, México (22°07'08"N, 86°52'03"W), ICMyL-UNAM 4.95.11; 1 specimen, Puerto Morelos, Quintana Roo, México (20°51'08"N, 86°51'06"W), ICMyL-UNAM 4.95.12.

Diagnosis.—Test broad, with elongate outline. Peristome broad (14 to 18% of TL). Periproct vertically elongated; distance from lower portion of periproct to adoral portion of subanal fasciole usually equal to, or greater than, the vertical diameter of the periproct.

Description.—Test broad anteriorly emarginated; the posterior contour is almost truncated and oblique in its end. Reddish brown test, covered with short and striated spines. Naked test brownish, brown or earth brown color. Apical system anterior, ethmolytic, each of the four genital plates bears a gonopore; two posterior plates are larger and more widely separated. Large tubercles on aboral surface scant, widely dispersed, distributed within the peripetalous fasciole. Small tubercles numerous, distributed over entire surface. Tubercles of the oral surface relatively enlarged, irregularly distributed. Anterior and posterior ambulacral grooves deep and narrow. Length of ambulacral grooves variable: some specimens with ones on right side longer, others with those of left side longer. Anterior ambulacral grooves curved backward. Posterior ambulacral grooves slightly longer than anterior ones. Scarce miliar granules occur on external edge of poriferous zone, between pairs of pores. Peristome anterior, sunken, narrow (14.4 to 17.6% of TL); anterior edge semicircular, keeled labrum. Periproct vertically elongated (17.75 mm mean height, 11.73 mm mean width). Peripetalous fasciole narrow, angular in course around petals. Subanal fasciole incomplete

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Figs. 1–6. Comparison of denuded tests of both subspecies. 1. *Meoma ventricosa ventricosa*, dorsal view; 2, peristome; 3, periproct. (Test length 134.56 mm), Puerto Morelos, Quintana Roo, México (20°51'03"N, 86°51'07"W), (ICMyL-UNAM 4.95.1). 4. *Meoma ventricosa grandis*, dorsal view; 5, peristome; 6, periproct., (test length 122.19 mm), Playa Las Gatas, Zihuatanejo, Guerrero, México, (ICMyL-UNAM 4.57.0).

in adults, enclosing a small area compared with *M. ventriocosa grandis*.

Distribution.—Fort Lauderdale, Florida, and the Bahamas Islands, southward through the Greater and Lesser Antilles; in the Gulf of México from southern Florida westward to Central America; the Orinoco River is the southern limit of this subspecies (Hendler et al. 1995). In Mexican waters it has been collected in Mérida, Yucatán (Serafy 1979); Cabo Catoche, Isla Contoy and Puerto Morelos, Quintana Roo. Bathymetric distribution.—From the intertidal to 200 m.

Holotype.—Unknown.

Type locality.—"Antilles" (Lamarck 1816).

Meoma ventricosa grandis Gray, 1851 Figs. 4–6, Table 1

Meoma grandis.—Gray 185: 132; Verrill 1867: 302; Agassiz 1872-74: 142; H. L. Clark 1917: 220; L. Boone 1928: 12; Zie-

Table 1.—Statistical summary. Coefficients of simple and multiple regression analysis of M. ventricosa s.s. (n = 9) and Meoma ventricosa grandis (n = 9). (Abbreviations in section of methods). Statistical significance level 95%.

Variables	Meoma ventricosa ventricosa		Meoma ventricosa grandis	
	Correlation coeff.	r ²	Correlation coeff.	r²
TL-TW	0.991	0.983	0.605	0.366
TL-H	0.957	0.917	0.511	0.261
TW-H	0.937	0.878	0.596	0.355
TL-PW	0.987	0.974	-0.078	0.006
TL-TW-H	t-values	r^2	t-values	r ²
TL-TW	4.501	0.999	2.856	0.998
TL-H	1.188		0.647	

senhenne 1937: 236; U. S. Grant & L. G. Hertlein 1938: 130; H. L. Clark 1940: 344; J. Steinbeck & E. F. Ricketts 1941: 401; H. L. Clark 1948: 344; Caso 1949: 354; Mortensen 1951: 526; Madsen 1957: 476; Caso 1961: 300–303; Fischer 1966: U592; Caso 1983: 66.

Kleinia nigra.—Agassiz 1863-1869: 27. *Meoma nigra.*—Verrill 1867: 251; 1870: 93.

Macropneustes grandis.—Cooke C. W. 1959: 83.

Meoma ventricosa grandis.—Chesher 1970: 745.

Material examined.—2 specimens, Acapulco, Guerrero, México, ICMyL-UNAM 4.57.1; 7 specimens, Playa Las Gatas, Zihuatanejo, Guerrero, México, ICMyL-UNAM 4.57.0; 1 specimen, outside of the Laguna de Yavaros, Sonora, México, ICMyL-UNAM 4.57.2, and 2 specimens from Magdalena Bay, Baja California Sur, México, not in catalogue.

Diagnosis.—Test with broad outline; peristome broad (19 to 22% of TL). Periproct almost circular. Distance from lower portion of periproct to adoral portior of subanal fasciole usually less than the vertical diameter of the periproct.

Description.—Dark brown test, covered with short, striated spines. Test wide and oval, anteriorly emarginated; posterior test

contour almost truncated and oblique in its end. Some specimens somewhat flattened, but majority arched at apex. Naked test light brown, dark brown or earth gray color. Apical system anterior, ethmolytic, each of the four genital plates possesses a gonopore; two posterior plates larger and more widely separated. Large tubercles on aboral surface scant and widely dispersed, distributed within the peripetalous fasciole. Small tubercles numerous, distributed over entire surface. Tubercles of the oral surface relatively enlarged, irregularly distributed, more tightly packed towards the anterior. Anterior and posterior ambulacral grooves wide (compared to those of Meoma ventricosa ventricosa). Anterior ambulacral grooves curved backward; in some specimens, length varies less than those of the posterior region (minimal variation 30 mm). Posterior ambulacral grooves slightly longer than anterior ones. Scarce, small miliary granules occur on the external edge of the poriferous zone, between pairs of pores. Peristome broad (19.1 to 21.1% of TL), anterior, sunken. Anterior edge formed by two lines converging on its anterior end, forming an obtuse angle, with lateral parts formed by small vertical lines. Labrum prominent, semicircular, not keeled; the posterior prolongation short. Periproct almost circular (16.8 mm mean high, 14.2 mm mean width).

Remarks.—Contour of peripetalous fasciole is highly variable in the observed specimens. The portion across the anterior interambulacral region varies less than other parts; nevertheless, in some specimens, the middle transverse portion is almost straight and in others it is slightly curved. Also, in some specimens it is folded at the level of the ambulacral groove; it generally folds over a small distance, forming a right angle on each side. In other specimens there are two bends, the second one larger than the first, near the anterior lateral grooves. As in M. ventricosa ventricosa, some of spines in the interambulacral zones are slightly curved. Large, primary spines are dark brown. In adult specimens, the average between the anterior genital pores is 1 mm, and between the posterior pores 2 mm.

Distribution.---Northern part of the Gulf of California (Angeles Channel, 29°01'05"N and 113°29'05"W) to Punta Choco, Puerto Utria, Colombia; Galapagos and Revillagigedo Islands. In the Gulf of Panama, outside Tortolita and Taboguilla Islands, at depths of 0.5-10 m (Mortensen 1951). In Mexican waters it has been collected in Punta Arena, Punta Gorda, Cabo San Lucas, Baja California; on the seaward side of Laguna de Yavaros, Sonora; Bahía Tenacatita, Jalisco; Playa Las Gatas, Zihuatanejo, Acapulco, Guerrero; Bahía Tangola Tangola, Bahía Santa Cruz, Oaxaca (Caso 1949, 1961, 1983). Chesher (1970) reports it from Bahía Santa Inés, Bahía Concepción, Gulf of California; Manzanillo, Colima; Acapulco, Guerrero; Puerto Huatulco, Oaxaca.

Geographic range extension.—Bahía Magdalena, Baja California Sur (24°35'00"N and 112°03'15"W); two adult specimens collected in the spring of 1991, on sandy bottoms, with an Ekman–Birge dredge at 26 m.

Bathymetric distribution.—From the intertidal to 100 m.

Holotype.—Meoma grandis (=M. ventricosa grandis Gray, 1851), The Natural History Museum, London, Catalogue number 1949.10.24.6.

Type locality.—Australia (locality which was taken from original label, the label no longer exists). The species is western Mexican and the locality Australia is therefore wrong (S. Halsey pers. comm. 1996). The original material was not labeled "Acapulco, México" as pointed out by Chesher (1970).

Statistical Analysis

Simple regression and correlation analysis showed that between the variables LT– TW, TW–H, TW–H (Table 1) in the case of *Meoma ventricosa* s.s. the correlation co-



Fig. 7. Multiple regression analysis of the test length (TL), test width (TW) and test high (H) of *Meoma ventricosa ventricosa*. $(r^2 = 0.999, n = 9)$.

efficients and the r^2 were highly significant. Otherwise, in the case of M. ventricosa grandis this correlation was relatively weak (Table 1). The above results were confirmed by multiple regression analysis of TL with respect to TW and H, which indicated that in the case of Meoma ventricosa s.s. fit of the regression line in the plot was more significant (Fig. 7) than in the case of M. ventricosa grandis (Fig. 8). The shape of the test in M. ventricosa s.s. tended to be more broad and anteriorly emarginated than in M. ventricosa grandis, which bears a wide and oval shape. The simple regression analysis between TL and PW for M. ventricosa s.s. showed a highly significant correlation, while that of M. ventricosa grandis was not significant (Table 1). The simple regression analysis of AH with AW for M. ventricosa s.s. showed a correlation coefficient (0.713)and r^2 (0.508) that indicated AH was significantly higher than AW. This is easy to recognize by simple observation of the specimens (Fig. 3). The simple regression analysis of AH with AW for M. ventricosa grandis showed a correlation coefficient (0.311) and r^2 (0.097) that indicated lack of



Fig. 8. Multiple regression analysis of the test length (TL), test width (TW) and test high (H) of *Meoma ventricosa grandis*. $(r^2 = 998, n = 9)$.

significance: the periproct is almost circular (Fig. 6). For the correlation analysis between AH and SAFT, the r^2 (*M. ventricosa* s.s. = 0.227 and *M. ventricosa grandis* = 0.181) didn't show a significant difference.

Descriptive statistics showed no significant difference between the two subspecies in analysis of TL versus width of the base of the tubercles for each ambulacral zone. r^2 was 0.99 in all cases. This character overlaps in both subspecies: *M. ventricosa* s.s., $\bar{X} = 1.03$, max = 1.4, min = 0.7 and *SD* = 0.152; *M. ventricosa grandis*, $\bar{X} = 1.02$, max = 1.4 min = 0.7 and *SD* = 0.114.

Discussion

Mortensen (1951) state that "only the characters of the primary tubercles of the aboral side, the frontal ambulacrum, and the peripetalous fasciole seem to afford reliable distinction between the two species". Chesher (1970) state that the differences between *M. ventricosa* s.s. and *M. ventricosa* grandis are the distance from the periproct to the adoral portion of the subanal fasciole compared with the vertical diameter of the periproct, and the distance from

the apical system to the lateral portion of the peripetalous fasciole.

In the present work, the statistical analyses showed following characters to be important in separating the two subspecies: 1) the shape of the test-in M. ventricosa s.s. it is broad and anteriorly emarginated, whereas in M. ventricosa grandis it is wide and oval; 2) the shape and size of the peristome-in M. ventricosa s.s. it is narrow, with the anterior edge semicircular and a keeled labrum, whereas in M. ventricosa grandis it is broad, with anterior edge formed by two lines converging on its anterior end and forming an obtuse angle, with lateral parts formed by small vertical lines, prominent labrum, that is semicircular and not keeled; 3) the shape of the periproct-vertically elongated in M. ventricosa s.s. and almost circular in M. ventricosa grandis.

We agree with Chesher (1970) that the distance from the periproct to the adoral portion of the subanal fasciole compared with the height of the periproct is important to separate the two subspecies.

Statistical analysis showed that the size of the aboral tubercles is not useful in distinguishing the two subspecies, as was also pointed out by Chesher (1970). It was shown by the same author that "this character is subject to ecological variation".

A new distribution range is now recognized for *M. ventricosa grandis*, extending to Magdalena Bay, Baja California Sur, México. This may be the northern limit of its distribution. This locality shows a special "faunistic conglomerate" that is transitional sub-tropical, with mingling of tropical and temperate faunas (Solís-Marín 1991). This transitional fauna does not prevail along the entire Baja California coast; in Magdalena Bay, a qualitative faunistic change is evident (Williams 1974). This change is explained by the influence of the California current (Loeb et al. 1983).

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